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MUTATION IN MATTHIOLA ANNUA, A "MENDELIZING" SPECIES[1]

Howard B. Frost

Interest in the subject of mutation seems to be growing, and with good reason. Varied as may be the processes concerned in the production of mutant forms, evidence is accumulating to show that sometimes, at least, mutation involves fundamental chemical or structural changes in the germ-plasm. It is obviously of great importance in practical breeding, and we cannot yet safely deny to it a significant rôle in evolution.

In view of the peculiarities in the general genetic behavior of Oenothera, it has become a matter of special importance to study mutation in plant forms that are known to exhibit typical Mendelian phenomena. Two general views of heredity in Oenothera appear still to be possible; first, the one recently expressed by Shull (1913), that regular segregation and recombination of genetic factors are absent; second, that the irregularity is secondary, and due to complicating influences, especially to selective sterility. Perhaps the genus possesses peculiarities of chromosome structure and behavior which will be found to justify a view practically intermediate between the two just stated.

It now seems very probable, whatever the fundamental reason, that other genera are to be classed with Oenothera as possessing certain genetic peculiarities. In Citrus, for instance, we find a similar tendency toward apparent mutation, which is very strikingly manifested by somatic tissues. Here, also, sterility seems to be common, as with the Washington navel orange, where it is complete in the anthers, and with the Satsuma mandarin, where very few of the pollen-grains are capable of germination. Probably the potato (or the genus Solanum?), with its apparent somatic mutation, its doubtfully regular genetic ratios, and its very general pollen-sterility, also belongs to this group.

If Oenothera is thus typical of a group of genera, we may expect to find this group characterized by a peculiar prevalence of hybridity. Apparently this hybridity is not due to unusual opportunities for interpollination of species in their past history; it is rather to be ascribed to an exceptional degree of fertility between decidedly unlike forms, perhaps combined with an unusual tendency to produce widely divergent forms by mutation. Frequent partial sterility of the resulting hybrids, sometimes producing *permanently heterozygous* forms, seems also to be a factor (de Vries, 1913).

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[1] Paper No. 27, Citrus Experiment Station, College of Agriculture, University of California, Riverside, California.

It has been urged that all the Oenothera mutations should be charged to hybridization. There is obviously a remarkable prevalence of hybridity in the genus, but we may well consider whether this hybridity may not be, in large part, a *result* rather than a *cause* of mutation.

However this may be, Belling (1914) seems to have shown that the artificial crossing of two "good species" may lead to the opposition (pairing), at the reduction division in the hybrid, of non-homologous genes, with the result that some germ-cells are not viable. That is, certain germ-cells may receive incompatible materials, or lack essential ones. If, then, a genus combines high mutability with wide limits of interfertility of forms, the resulting germ-plasms may be very unsymmetrical in the structure of their pairs of chromosomes, often producing non-viable gametes, and may therefore be apparently "non-Mendelian" in transmission of characters. It seems very significant, in this connection, that the various "species" of Oenothera and of Citrus are so generally interfertile.

Von Tschermak (1912) has made a specially extensive experimental test of the factor-hypothesis of heredity, and concludes that his evidence is very favorable to this hypothesis. One of the three plants which he used is the ten-weeks stock, *Matthiola annua* or *M. incana* var. *annua*, which Miss Saunders (1911) also has found to give typical Mendelian results for flower-color and pubescence. Mutations similar to those of Oenothera, occurring in such material, acquire a special significance.

In Annual Report 8 of the American Breeders' Association, I (Frost, 1912) reported the discovery of a series of such mutations in stocks, discussing especially a few-noded type of apparently regular heredity. Six or seven of these types have reproduced themselves in progeny-tests, some through several generations, but only the early (few-noded) type has been found to be evidently homozygous in any case, even in the later generations. With all the other types, a large part of the progeny, usually more than one half, always belong to the type ("Snowflake") from which the mutant types were originally secured.

Possible explanations of this peculiar transmission of the mutant types will be discussed in a paper now in preparation, and cannot be adequately considered here; lower viability of the mutant types, and linkage with the factor for the less viable single-flowering type[2] are obviously concerned in some cases. The point to be emphasized here is that this peculiar behavior occurs in a species which, as to certain other factors, is typically "Mendelian."

A brief characterization of eight of the mutant types, including all that have been proved to be hereditary, will be given. It should be noted first that the foundation stock consists of one variety only, a very uniform white-flowered glabrous "double-throwing" form, known as "Snowflake." As with other double-producing stocks, all the single-flowering plants are heterozygous for "doubleness," producing about fifty percent[3] of double progeny, while the doubles are totally sterile. The fact that the doubles form about one half of each generation, rather than one fourth, is due to the fact that all functional pollen is doubleness-carrying, or lacks some factor necessary to single (or normal) flowers.

The early type, which was described in Annual Report 8 of the American Breeders' Association, differs from Snowflake (figs. 1, 2 and 3) mainly or entirely in size-characters and earliness of flowering. The original early mutant was heterozygous. Twenty of its progeny have been tested; 4 of these were probably pure early, and 7 were obviously pure Snowflake. Presumably the mutation occurred in one germ-cell, which then united in fertilization with a normal Snowflake germ-cell. In the absence of complications, such a mutant would be expected to reproduce its type in about 75 percent of its progeny—as actually occurred with this type.

In striking contrast to this case, all the other mutant types identified are marked by peculiarities of leaf-form and of general habit, and no individual yet tested has proved homozygous.

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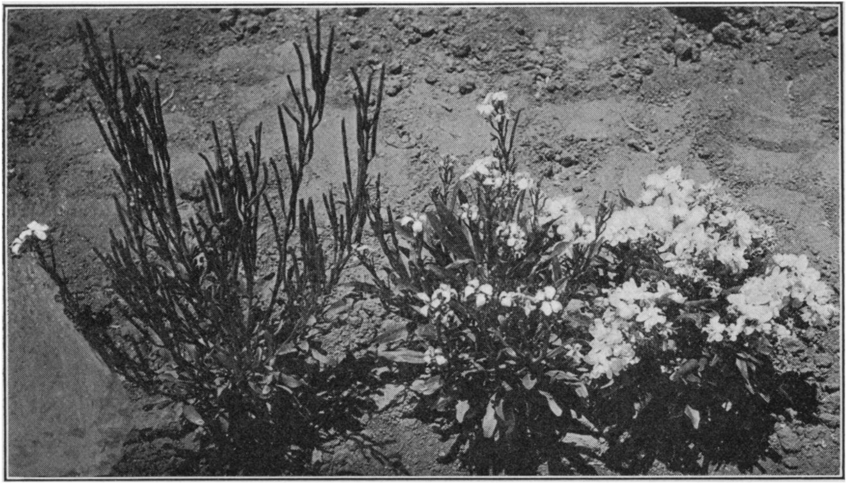
[2] The single-flowering plants appear somewhat less vigorous, and less resistant to some unfavorable conditions, than the double-flowering ones.

[3] There is the usual slight excess of doubles; 7,310 progeny of Snowflake parents included 53.037 percent of doubles.

One of the most interesting of all the mutant types is a *gigas*-type, designated "large-leaved" (fig. 1). This has leaves longer and thicker than those of the Snowflake type, with stout stem and capsules, and is late in blooming. About half of its progeny reproduce its type, while nearly all the rest are Snowflake. Evidence is not yet at hand to explain the deviation from the expected seventy-five percent of large-leaved progeny, though there are several evident possibilities.



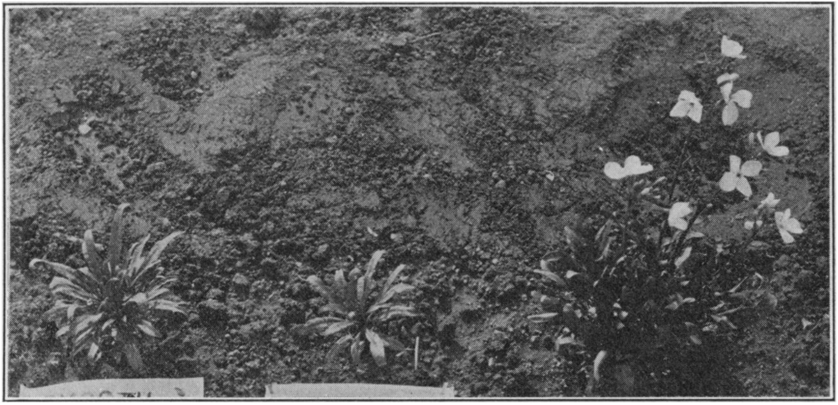
THE LARGE-LEAVED AND NARROW-DARK-LEAVED TYPES

FIG. 1. Matthiola plants at Riverside, California, in 1914–15. Progeny of a Large-leaved parent. Types, from left to right: Snowflake, Large-leaved, Narrow-dark-leaved. Observe especially the lateness of the Large-leaved plant (it should be noted that this type has seemed to seed quite as freely as Snowflake when grown to maturity under favorable temperature-conditions).

The smooth-leaved type (fig. 2) was named from the lack of buckling between the main veins in the leaves of young seedlings grown in the greenhouse. In field cultures, with injuriously high temperature and at times deficient moisture, the leaves become dotted with small brown spots. Flowering is late, and the mature stems are brittle. Probably the fibrovascular system is in some way defective.

The crenate-leaved type (fig. 3) has more crenation or serration of the leaf-margins than has Snowflake, under some conditions much more; the plants are small and slender, and under unfavorable conditions may be extremely dwarfed.

The narrow-leaved type is characterized by rather rigid narrow leaves, flat or concave upward, ascending rather than horizontal; the sepals and petals are conspicuously narrow. The narrow-dark-leaved type (fig. 1) is in some respects more like Snowflake; its leaves tend to be small, very dark green, and smoothly convex upward, while the sepals are probably normal. Two variant parents, grown before this last type was recognized, have given it among their progeny; one of these, however, apparently gave four to six other definite types, including Snowflake as usual.



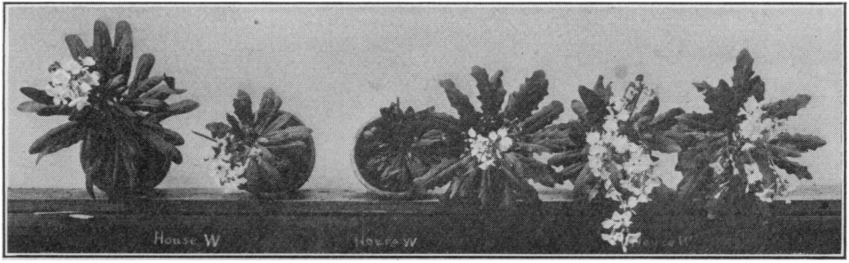
THE SMOOTH-LEAVED TYPE

FIG. 2. Matthiola plants at Riverside, California, in 1913–14. Progeny of a Smooth-leaved parent. Types, from left to right: Smooth-leaved, Smooth-leaved, Snowflake. Note the lateness of the Smooth-leaved plants, and the punctate appearance of some of the leaves (due to small dead spots.)

The slender type, under favorable conditions, is much like Snowflake, but with somewhat lengthened internodes, petioles, and pedicels. Under some unfavorable conditions it may be much dwarfed, although it seems to endure high temperatures better than Snowflake. Two grades of this type have been found; the extreme form, in one small test, gave the larger proportion of slender progeny, but still only nine plants out of sixteen. In this last case the plants were all doubles, and elsewhere there is, apparently, linkage of a specially puzzling sort with the single-double factor-pair.

The last five types described have all given considerably less than 50 percent of mutant-type progeny.

The small-smooth-leaved type is the smallest and weakest of all that have been named. Two individuals, both singles, have flowered, but no seed was produced. Several other forms have been named, but have failed to give seed; it is very probable that at least two or three of these are definite genetic types, distinct from any discussed above. In fact, it is not improbable that as many as fifteen distinct genetic types have been observed, some perhaps only once among about 8,000 plants.



THE CRENATE-LEAVED TYPE

FIG. 3. Matthiola plants grown in greenhouses at Ithaca, N. Y. Progeny of Snowflake parents. Types: one Snowflake plant at the left in each row, the rest Crenate-leaved mutants. Note the crenation or serration of the leaf-margins, which here is nearly absent with Snowflake but usually very marked with Crenate-leaved.

Many Snowflake parents have given mutant progeny. The number of apparent mutants, under favorable conditions for germination and growth, was about four or five percent of the whole number of progeny. The commoner forms appeared many times, as progeny of many parents; it seems probable that any Snowflake parent, self-pollinated, can give rise to any of the mutant types studied. It is, however, probable that plants of some mutant types produce other mutant types more frequently than does Snowflake.

The mutant individuals are obviously not extracted pure recessives, but heterozygous dominants. Since they have occurred many times in cultures from selfed parents, they are not due to combination of complementary factors by cross-fertilization. They would seem, then, to be due to definite changes in the germ-plasm, changes distinct from those shiftings which produce ordinary Mendelian phenomena. Whether past hybridization has made these mutative changes possible, is an open question; we know that new types may be formed by hybridization, but the known methods of such type-formation seem to be out of the question here.

Finally, it should be noted that in most of these cases the mutative change has far-reaching effects, modifying various characteristics of the plant. Notwithstanding this fact, the factor for the new type is regularly inherited as a unit, and sometimes shows linkage with another factor-pair, so we may suppose that the essential change is limited, in some cases at least, to a portion of one chromosome.

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